FORUM COMMENT

Is bird song a reliable signal of aggressive intent? A reply

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Abstract We advocate assessing the reliability of signals
of aggressive intent by eliciting aggressive signaling from a
subject, giving the subject an opportunity to attack a model,
and testing whether the subject's displays predict a
subsequent attack. Using this design, we found that most
singing behaviors are poor predictors of attack in song
sparrows (*Melospiza melodia*). Laidre and Vehrencamp
(*Behav Ecol Sociobiol*, DOI 10.1007/s00265-007-0539-3,
2008) suggested altering our experimental design to make
the model more realistic; it remains to be seen whether such
design changes would change the association between
display and attack. Laidre and Vehrencamp (*Behav Ecol
Sociobiol*, DOI 10.1007/s00265-007-0539-3, 2008) also
suggested that the reliability of soft song, the one display
that predicts attack in song sparrows, can be explained by a
vulnerability cost. We question the rationale for a vulner-
ability cost for this display and suggest instead that soft
song has a competing functions cost, in that, by using soft
song to counter an intruder, a male sacrifices other possible
functions of vocal signaling.

Keywords Animal communication · Reliability · Soft song ·
Vulnerability

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Introduction

Laidre and Vehrencamp (2008) raised two issues regarding
our recent paper on the reliability of song as a predictor of
attack in song sparrows (*Melospiza melodia*; Searcy et al.
2006). The first concerns the correct explanation for the
reliability of soft song, the one display that proved to
predict attack in this study. The second concerns whether
changing the experimental design of the study might alter
our overall conclusion that singing behaviors and other
displays are not good predictors of aggression in this
species. We will discuss both issues, starting with the latter
point on experimental design.

Designing experiments on aggressive signaling

In earlier studies, the aggressiveness of singing behaviors in
songbirds has been assessed using "territorial playback", in
which signals are played to male birds on their territories
and their aggressive response is measured, with the
assumption that subjects respond most strongly to the most
aggressive signals. Evidence suggests, however, that the
opposite pattern sometimes holds, that is, subjects some-
times respond most strongly to less aggressive signals
(Searcy and Nowicki 2000). Both patterns are readily
interpretable: An individual might respond more strongly
to a more aggressive signal because it is perceived as a
more important challenge, or an individual might respond
more strongly to a less aggressive signal because the
contest appears easier to win. Because the results of
territorial playback are ambiguous with respect to the
aggressive meaning of song, we have advocated an
alternative experimental design, in which aggressive dis-
play is elicited from a subject, the displays are recorded,

and the subject is subsequently given an opportunity to attack a model stimulus. Analysis then examines whether prior displays predict subsequent attack. Studies using such a design include Waas (1991a) with little blue penguins (*Eudyptula minor*), Capp and Searcy (1991) with bobolinks (*Dolychonyx oryzivorus*), and the study that is the focus of Laidre and Vehrencamp's commentary, Searcy et al. (2006) with song sparrows.

Laidre and Vehrencamp (2008) were not critical of this general approach but rather of some of the specifics of the experimental design used by Searcy et al. (2006). In that study, we elicited aggressive signaling from a territorial male song sparrow using 1 min of playback of one of the subject's own song types. Starting with the first playback song, we recorded the subject's display behavior for a 5-min initial recording period. At 6 min into the trial, we revealed a taxidermic mount of a song sparrow, in a normal perched posture, coupled with another 2 min of playback. The subject was given another 14 min to attack the mount, while we continued to record its displays. Out of 95 subjects, 20 attacked the mount. None of the six display features we measured differed significantly between attackers and nonattackers in the initial recording period. For the 1-min preceding attack, attackers gave significantly more soft songs than nonattackers did, and a discriminant function based on soft songs correctly classified 74% of subjects as attackers or nonattackers. Song type matching and song type switching, two behaviors that have been hypothesized to be graded signals of aggression (Krebs et al. 1981; Kramer and Lemon 1983; Kramer et al. 1985), did not differ between attackers and nonattackers in either time period and did not enter discriminant functions predicting attack.

Laidre and Vehrencamp (2008) suggested three changes to this design that they think might strengthen the association between displays and attack. The first two changes involve making the model used to elicit aggression more realistic, by giving it a more aggressive posture and by making it more interactive, so that it could escalate its apparent aggressiveness during the trial. Laidre and Vehrencamp (2008) hypothesized that the nonaggressive posture and static behavior of the model we used might have elicited abnormal and inconsistent behavior from the subjects and that these problems might have prevented our seeing a consistent relationship between displays and subsequent aggression.

This argument is weakened by results from a recent study by Ballentine et al. (2008), which used the same design as in Searcy et al. (2006), including a static nonaggressive model, and which found quite strong relationships between displays and attack. This new study was done with swamp sparrows (*Melospiza georgiana*), one of the song sparrow's closest relatives. Soft song was again the display that best predicted attack in swamp sparrows,

but otherwise results were rather different. Whereas in song sparrows no display in the initial recording period differed between attackers and nonattackers, two differed significantly in swamp sparrows—wing waves and soft songs. These two displays also both differed significantly between attackers and nonattackers in the 1 min prior to attack. Discriminant functions based on displays were significant predictors of attack both for the initial recording period and the 1 min prior to attack, correctly classifying as many as 85% of subjects as attackers or nonattackers. Thus, the unnatural behavior of the model serving as the focus of attack did not prevent there being a consistent association between display and attack in this second study on a related species.

Nevertheless, we agree that it would be instructive to incorporate the two design changes proposed by Laidre and Vehrencamp (2008) in future experiments with song sparrows. Laidre and Vehrencamp (2008) suggested that one way the model could be made more realistic is by making it mobile using a rope-and-pulley system. We have been working on an alternative method of making the model mobile: We have built a "robotic sparrow" consisting of a taxidermic mount fixed to a small radio-controlled motorized chassis. The chassis is housed in a 1.0-m-long tunnel with a slot in the roof through which extends a dowel that holds the mount. The tunnel both conceals the chassis and constrains it to move in a straight line. When the actuator is activated remotely, the model moves quietly forward or backward under its own power. A second actuator is activated remotely to change the direction the model faces. In pilot trials, male song sparrows seemed to behave normally toward this robot. Thus far we have not found a dramatic increase in attacks in response to either an advance or a retreat by the model. We have not yet tested whether attacks are more predictable with this mobile stimulus but plan to do so.

Modeling an effective and active aggressive posture is more difficult, but we are now developing a robotic sparrow that can wing wave. Wing waving is a visual display used by both song and swamp sparrows, in which the wing is held away from the body and vibrated rapidly (Nice 1943; Nelson and Marler 1989). In our experience, wing waving is the postural display most closely associated with aggressive contexts in both song and swamp sparrows, though this behavior only predicts attack in the latter group (Ballentine et al. 2008). With a robotic sparrow that wing waves, we can test whether the aggressiveness of song sparrows is affected by this display and whether attack is better predicted by other displays when the model wing waves than when it does not.

The third design change suggested by Laidre and Vehrencamp (2008) is to decrease the time interval between the displays analyzed and the aggressive behavior they are

asked to predict. Searcy et al. (2006) found in song sparrows that the displays given during the 1 min immediately before attack were better predictors of which subjects would attack than displays given in the earlier 5-min recording period. The explanation we suggested was that contingencies that arise in the interval between display and attack weaken their association and that the longer the interval the more such contingencies arise. Ballentine et al. (2008), however, found a different pattern of results in swamp sparrows: Displays in the earlier period were just as good predictors of attack as displays in the later period. Moreover, we have found that individual male song sparrows are consistent across days in both aggressiveness and display patterns such as use of soft song (Nowicki et al. 2002; Hyman et al. 2004; Searcy and Nowicki 2006). Consistency across days implies that these behaviors are not much influenced by external events. Furthermore, when we look more deeply at how display rates change over time in song sparrows as attack approaches, we do not find evidence that displays escalate leading up to attack. Figure 1 shows previously unpublished data from the study of Searcy et al. (2006) on rates of soft song in the subset of males that eventually attacked the model. No increase is seen as attack approaches. Results on other display features are similarly negative. If the subset of males that eventually attack does not escalate their display behavior leading up to attack, then it does not seem likely that displays given just preceding attack will be better predictors than displays given earlier.
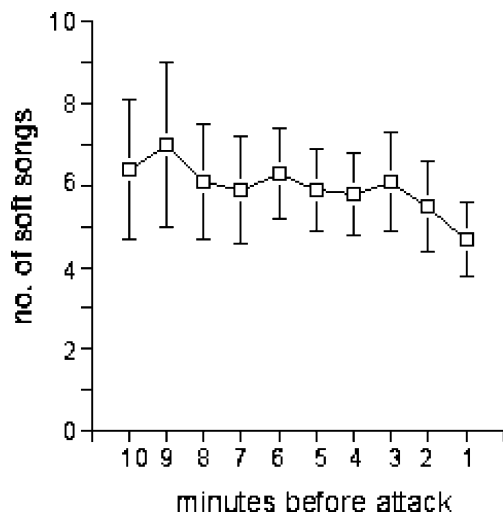

Fig. 1 Mean numbers of soft songs (±SE) leading up to attack in song sparrows. Data are from a subset of the 20 males that eventually attacked the model in Searcy et al. (2006). Only the 14 males that waited at least 2 min to attack are included, so that each male contributed data to at least min 1 and 2. Sample sizes decrease from 14 in min 1 and 2 to five in min 10

The cost of soft song

The other issue raised by Laidre and Vehrencamp (2008) concerns how to explain the reliability of soft song as a predictor of attack, an issue not considered by Searcy et al. (2006). Laidre and Vehrencamp (2008) favored a hypothesis that was previously discussed by Vehrencamp (2000) and Ballentine et al. (2008): that soft song imposes a vulnerability cost and thus can be considered a vulnerability handicap. A signal has a vulnerability cost if "the execution of the signal necessarily places the sender in a position of vulnerability to attack and injury by the receiver" (Vehrencamp 2000). This criterion is not met by soft song, which can be and sometimes is produced at a considerable distance from the receiver, nor does performance of soft song move the signaler closer to the receiver or uncover a vulnerable part of its body, as is argued for some postural displays (Waas 1991b). Instead, the argument for vulnerability rests on the fact that a signaler has to be close to a receiver for its soft song to be perceived, with the consequence that "this signal unavoidably advertises how close a bird is willing to come to its rival" (Laidre and Vehrencamp 2008). Loud song produced close to a receiver, however, is actually a less ambiguous signal of proximity than is a low-amplitude song (Ballentine et al. 2008). Because all sounds attenuate with distance, a song that is still loud when it reaches the receiver must have been produced nearby, whereas a song that is of low amplitude when it reaches the receiver could be a soft song produced nearby or a louder one produced further away. Because soft song neither necessarily opens a signaler to attack nor signals proximity better than loud song, we do not think the vulnerability cost hypothesis is tenable for this signal.

As a test of the vulnerability cost hypothesis, Laidre and Vehrencamp (2008) suggested a playback experiment that would contrast response to the loudest soft songs played from far away to response to the softest soft songs played nearby, arranged so that the amplitudes would be equal when the signals reached the subject. We agree that this would be an interesting experiment, though controlling amplitude of the signal at the subject would be difficult to accomplish more than momentarily. We feel, however, that such an experiment is better thought of as a test of a receiver retaliation cost (Vehrencamp 2000) than of a vulnerability cost. A receiver retaliation cost results when one signal is more likely to elicit an aggressive response from an opponent (especially the strongest, most aggressive opponents) than is an alternative signal. One way of thinking about the difference between receiver retaliation and vulnerability handicaps is that in the former case the signal increases the likelihood of attack by a given opponent, whereas in the latter case the signal increases the cost (in injury) per attack. Thus, an experiment that asks

which of the two signals is more likely to be attacked is really a better test of receiver retaliation and is usually interpreted as such (Vehrencamp 2001; Anderson et al. 2007).

Another possibility is that reliability is maintained by a "competing functions" cost, a kind of cost that arises when altering signals to maximize one function depresses another competing function (Anderson et al. 2007; Ballentine et al. 2008). Such a cost arises directly from the feature that defines soft song, its low amplitude. Low amplitude is costly to the signaler because it prevents the signal from being perceived by any but the closest receivers. Because of the signal's low amplitude, a territorial intruder that perceives the signal can be sure that it is directed at him alone and thus that the singer's attention is focused on him. Evidence that limiting the active space of song is costly to the singer comes from another study with song sparrows (Searcy and Nowicki 2006). In this study, we simulated singing interactions on territories, in which loud intruders were countered by owners singing either loud songs or soft songs. Intrusion by other "third party" males was more common and more prolonged when the simulated owner used soft song than when it used loud song. Presumably, this effect occurs because males off the territory cannot perceive the territory owner's soft songs and thus cannot tell that he is countering the intruder. Thus, an owner using soft song to counter one intruder pays a cost by encouraging intrusions by other males.

Conclusions

Laidre and Vehrecamp (2008) concluded that it is premature to decide based on the results of Searcy et al. (2006) that song is a poor predictor of attack in song sparrows, as this conclusion might be reversed if an experiment was set up in a different way. Again, we agree that this is an intriguing possibility and promising enough that we are interested in pursuing it. A couple of notes of caution are in order, however. It seems logical that making the model that elicits attacks more realistic would have the effect of raising the frequency of attacks, but our preliminary results working with a mobile mount make us somewhat skeptical even of this. Even if making the model more realistic does increase the likelihood of attack, it is not necessarily true that the association between display and attack will be strengthened. We suspect that, whatever the details of the experimental design, some signals that have been posited to be "graded signals of aggression," such as song type matching and type switching, will turn out to contain no information on attack likelihood. At any rate, we suggest that the general experimental approach we have used is the correct way to answer these questions: To elicit aggressive displays from

the animal, give it an opportunity to attack an experimental stimulus, and then test the strength of the association between display patterns and attack.

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